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SPECIAL FEATURE: REVIEW

Rapid Adaptation

Evolutionary ecology of learning: insights from fruit flies

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Abstract Ecologically and evolutionarily oriented research on learning has traditionally been carried out on vertebrates and bees. While less sophisticated than those animals, fruit flies (*Drosophila*) are capable of several forms of learning, and have the advantage of a short generation time, which makes them an ideal system for experimental evolution studies. This review summarizes the insights into evolutionary questions about learning gained in the last decade from evolutionary experiments on *Drosophila*. These experiments demonstrate that *Drosophila* has the genetic potential to evolve a substantially improved learning performance in ecologically relevant learning tasks. In at least one set of selected populations, the improved learning generalized to a task other than that used to impose selection, involving a different behavior, different stimuli, and a different sensory channel for the aversive reinforcement. This improvement in learning ability was associated with reductions in other fitness-related traits, such as larval competitive ability and lifespan, pointing to evolutionary trade-offs for improved learning. These trade-offs were confirmed by other evolutionary experiments where a reduction in learning performance was observed as a correlated response to selection for tolerance to larval nutritional stress or for delayed aging. Such trade-offs could be one reason why fruit flies have not fully used up their evolutionary potential for learning. Finally, another evolutionary experiment with *Drosophila* provided the first direct evidence for the long-standing idea that learning can under some circumstances accelerate and in others slow down genetically based evolutionary change. These results demonstrate the usefulness of fruit flies as a model system to address evolutionary questions about learning.

Keywords Behavior · *Drosophila* · Experimental evolution · Learning · Memory · Trade-offs

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Introduction

Learning involves acquisition and storage of information. However, we cannot directly access the neural representation of past experience in the memory of an animal, nor can we ask it to tell us what it remembers. It is thus only through a change of behavior that we can find out that the animal has learned something. More importantly, any benefits of the learned information or skill for fitness can only be realized through behavior. Therefore, in biology, learning is usually operationally defined as a change in an animal's behavior resulting from a past sensory experience that the animal remembers. Defined this way, the process of learning consists of three stages: acquisition of information, its storage in memory, and, at some later time, its retrieval, which leads to a change in behavior.

Learning is often regarded as a form of adaptive phenotypic plasticity, but learning actually differs from other forms of plasticity in an important way (Dukas 2004a). Plasticity means that the phenotype expressed by an individual is affected by its environment in addition to its genotype (Fig. 1a); this relationship between the phenotype and the environment is described by the reaction norm (Stearns 1992; Schlichting and Pigliucci 1998). Plasticity can become adaptive as a result of natural selection acting on genetic variation in the shape of the reaction norm, favoring responses that lead to high fitness in each

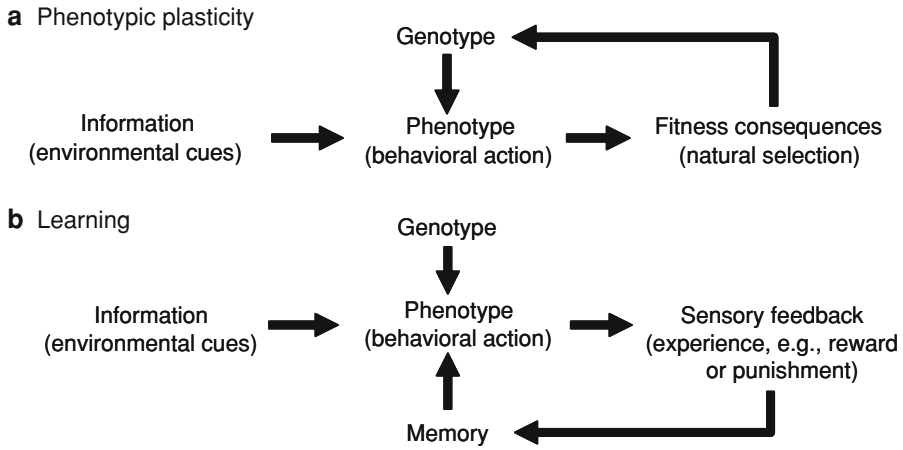

Fig. 1 Schematic comparison between adaptive phenotypic plasticity of behavior (**a**) and learning (**b**). The feedback that makes plasticity adaptive is provided by natural selection acting over generations at the level of the population. In contrast, adaptive learning responses develop within the lifetime of an individual based on the feedback provided by sensory information

environment. An example of such adaptive plasticity in behavior is the response of many birds of temperate regions to changes in photoperiod. Many of them respond to increasing day length at the end of winter by switching on behaviors anticipating breeding, such as courtship or territoriality. Conversely, decreasing day length at the end of summer induces migratory behavior in species that could not survive winter in their breeding range. These responses are obviously adaptive, as they allow the animal to anticipate the beginning of the breeding season or the coming of winter before the breeding or winter conditions actually arrive. Such an adaptive plastic response develops over generations through the action of natural selection on genetic variation in the reaction norms. Adaptive plastic responses of this type are thus specific to the environmental factors as well as to the phenotypes affected.

In contrast, learning relies on general neural mechanisms that integrate sensory input. In learning, the phenotype—the behavioral action the individual takes—not only depends on the genotype and the current environment, but also on the memory of past events, such as the consequences of choosing particular actions in similar circumstances in the past (Fig. 1b). Thus, in contrast to a "classic" adaptive plastic response, a learned response develops within the lifetime of an individual based on sensory feedback. This general learning machinery can be applied to new problems and challenges; it allows an animal to develop, within its lifetime, an adaptive response to a completely novel situation that has never been encountered in the evolutionary past of the species. For example, birds can quickly learn to press a lever or peck at particular geometric shapes to receive food, even though those shapes or levers are not encountered in the natural environment. Without learning, the development of such a response would require many generations of natural selection. Thus, in a sense, learning makes natural selection on behavior obsolete.

Similar to any complex adaptation, the ability to learn is itself a product of evolution driven by natural selection. Because of this extraordinary flexibility, which can only be compared to the flexibility of the vertebrate adaptive immune system, the ability to learn can be regarded as one of the top achievements of biological evolution. Furthermore, no other species is as dependent on learning and its generalization—intelligence—as ourselves. Understanding when, how, and why evolution produces improvements in learning ability would thus offer important insights into our own origin and nature.

Many decades of research on animal learning carried out by comparative psychologists have revealed that most animals are capable of some forms of learning. Concomitantly, neuroscience has identified foci of learning in the brain and has made inroads into understanding its neuronal and molecular bases. More recent decades have seen the emergence and development of cognitive ecology, which focuses on the functions of learning in nature and on adaptive differences in learning skills between populations and species in relation to their ecology (Shettleworth 1999; Healy and Braithwaite 2000; Reader and Laland 2002; Dukas 2004a). This research program has revealed that learning plays an important role in the natural lives of many animal species, vertebrate as well as invertebrate. For example, many animals memorize landmarks to navigate in their environment (Dyer et al. 2008; Merkle and Wehner 2008; Odling-Smee et al. 2008). Some mammals and birds cache food for the winter; careful studies show that Clark's nutcrackers can memorize the locations of several thousand food caches (Kamil and Jones 1997). Predators use associative learning to develop avoidance of toxic or distasteful prey (Gittleman and Harvey 1980; Ihalainen et al. 2008), while parasitoids learn which plant volatiles lead to vulnerable host individuals (Bleeker et al. 2006). Operant learning (trial-and-error learning of a skill), which allows animals in captivity to learn to press a lever or peck at geometric symbols to retrieve food (e.g., Ono et al. 2002), allows them to learn for example how to collect nectar from novel flower species or how to handle novel prey

items in nature (Chittka and Thomson 1997). While the above examples involve animals learning from their own experience, some animals rely on learning from others (i.e., social learning). For example, most songbirds learn their song by listening to their father (Beecher and Brenowitz 2005), but birds may also learn where to find food by observing other species (Seppanen and Forsman 2007). Finally, a combination of innovation with social learning, which forms the basis of our civilization, can also be observed in some other vertebrates; examples include the use of hammers of wood or stone to crack nuts by chimpanzees (Boesch et al. 1994) or food washing in Japanese macaques (Nakamichi et al. 1998). Even though the benefits of learning for fitness in natural environments have only rarely been demonstrated experimentally (but see Dukas and Bernays 2000; Dukas 2004b; Raine and Chittka 2008), they can be plausibly inferred and are intuitively well understood.

However, the benefits of learning are but one aspect of the evolutionary ecology of learning; several other relevant issues have remained relatively unexplored. First, we do not know how much genetic variation in learning ability is present in natural populations; yet this variation is the raw material of evolution and so determines the potential of a species to evolve improved learning performance. Second, the extent to which evolution acts on general aspects of learning mechanisms versus more or less independent modules that are specific to particular learning tasks and contexts is a controversial subject (Healy and Braithwaite 2000; Bolhuis 2005). Third, we know little about the evolutionary costs and trade-offs associated with learning, although it is the balance of these benefits and costs that determines whether natural selection favors improved learning. Finally, even though it was proposed over 100 years ago that learning affects genetically based evolutionary change (Baldwin 1896; Osborn 1896), this idea remained untested until recently.

These issues are most directly addressed with evolutionary experiments, which allow one to study in real time evolutionary changes in replicate experimental populations subject to controlled selection regimes. The species that have traditionally been the focus for studies of animal learning in an ecological context—mammals, birds, fish, bees—are not well suited to this approach: they have long generation times, and the maintenance of a large population of such a species under controlled conditions is impractical. For these reasons, we chose to use fruit flies (*Drosophila melanogaster*) as a study system. Fruit flies have been a favorite model system for experimental evolution studies—they are short-lived (their generation times can be as short as 2 weeks) and easy to maintain in large numbers under standard conditions. While their learning prowess falls short of that of honey or bumble bees (not to mention vertebrates), they are capable of several forms of learning, and in the last two decades they have become *the* favorite system for discovering genes whose products are involved in the learning processes (Davis 2005). While many other small and short-lived insect species might be equally suitable for evolutionary experiments on learning, using *Drosophila melanogaster* allows one to access the wealth of genetic information and the genetic toolkit developed for this model system. It also allows the results of evolutionary experiments to be integrated with the knowledge of the neurobiology of this species. In this paper I summarize the insights that experimental research on learning in *Drosophila*—much of it done in our laboratory—has offered concerning the four issues enumerated above.

Genetic potential for improved learning

If learning and intelligence are beneficial, what constrains the evolution of improved learning abilities? One could speculate that, in most species, natural selection would favor improvements in learning performance, but the response to selection is constrained by a lack of relevant genetic variation. Maybe the neuronal machinery involved in learning is already so complex and fine tuned that it is difficult to improve, and so new alleles that would confer such improvements only occur very rarely. Alternatively, one might imagine that most species do harbor genetic variation that would allow them to evolve better learning abilities, but in nature this potential is not used by evolution because the costs would be greater than the benefits. Thus, according to the first of these two hypotheses, the evolution of learning would be constrained by genetics, whereas the second hypothesis assigns more importance to ecology, as it is the ecology of the species that would determine the relative importance of the benefits and costs of learning from the viewpoint of Darwinian fitness.

The first of these hypotheses can be addressed by imposing laboratory selection regimes on experimental populations and determining to the extent to which their learning performances can be improved. In our laboratory we tested if a typical nature-derived population of fruit flies has the genetic potential for a marked improvement in learning performance in an ecologically relevant associative learning task. We subjected replicated populations to a selection regime that favored the flies' ability to associate a flavor of an oviposition substrate with an aversive bitter taste (Mery and Kawecki 2002). For each generation, the flies were given a choice between two oviposition substrates, made of orange and pineapple juice. The first time they encountered these substrates

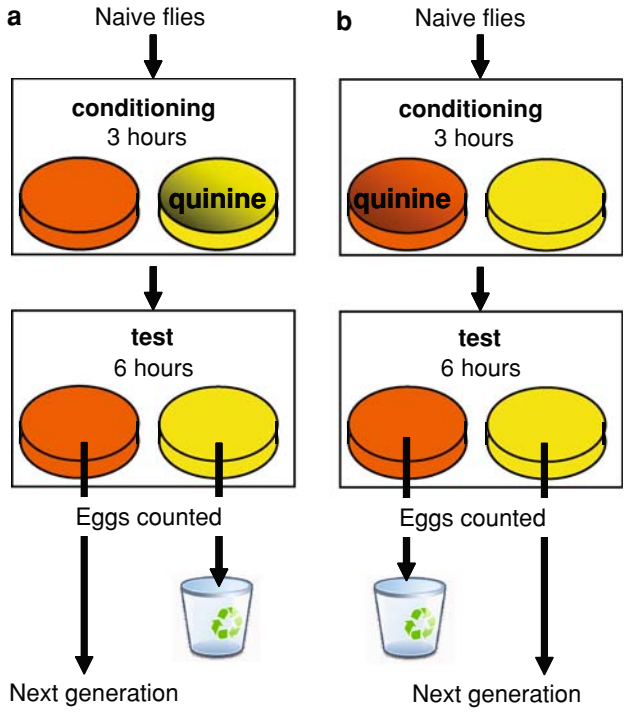

Fig. 2 The oviposition learning assay. During the conditioning period the flies have the opportunity to associate the flavor of the substrate (orange or pineapple) with the bitter taste of quinine; the other substrate does not contain quinine. During the test period the two substrates are again offered, but quinine is no longer present. The difference between the proportions of eggs laid on the orange substrate by flies conditioned with quinine + pineapple (**a**) versus flies conditioned with quinine + orange (**b**) is used as a learning score. To impose selection for learning, the next generation is exclusively bred from eggs laid in the test period on the substrate that did not contain quinine in the conditioning period. Modified from Mery and Kawecki (2002)

(conditioning period, Fig. 2), one of them (say, pineapple) was supplemented with quinine, the taste of which is aversive to flies, although they cannot smell it because it is not volatile. The flies had thus an opportunity to learn that one of the fruit odors leads to a high-quality resource while the other is associated with a bitter, unsuitable resource patch. After 3 h, a new set of orange and pineapple substrates was offered, with neither containing quinine this time (test period, Fig. 2). The flies that remembered which substrate was bitter previously would continue to avoid this substrate even though the quinine was not present this time, and would instead preferentially lay their eggs on the other substrate. Their learning ability would thus be reflected in the distribution of eggs laid in the test period on the two substrates. We quantified the learning ability with a learning score, defined as the difference between the proportion of eggs laid on the orange substrate by flies previously conditioned to avoid pineapple and the analogous proportion laid by another group of flies previously conditioned to avoid orange. The maximum learning score is thus one, and a value of zero means no learning. To impose selection for improved learning, the next generation was bred from eggs laid during the test period on the substrate that did not contain quinine (i.e., was of good quality) during the preceding conditioning period. In this way, flies that remembered which substrate had been good contributed more genes to the next generation. The identity (orange vs. pineapple) of the "good" substrate alternated between generations (for details see Mery and Kawecki 2002). All flies were bred on a standard cornmeal medium, so they only encountered the orange and pineapple substrates during the conditioning and test periods.

The base population from which the selected populations originated did not show any detectable learning in this assay, and this remained the case for unselected control populations. In contrast, within two dozen generations the populations subject to the above selection regime all evolved a robust learning response. Further assays indicated that flies from the unselected control populations are capable of some degree of learning (it would be surprising if they did not). With a sufficient amount of conditioning they were able to reach similar learning scores to the selected populations, but the flies from the selected populations learned faster (Fig. 3a). They also remembered longer—they still showed a detectable preference for the substrate that had previously contained quinine after a "forgetting interval" of 3 h; in contrast, the control populations lost most of their responses when the conditioning and test periods were separated by a 1-h interval (Fig. 3b).

Thus, our selected populations had the potential to evolve, within a few dozen generations, a substantially improved performance in an ecologically relevant, female-specific learning task. Another evolutionary experiment (Reif et al. 2002) addressed the recognition of unreceptive females by males, which to a large degree is a learned behavior. After 21 generations, populations where the two sexes interacted over 2 weeks became better at this male-specific learning task than populations subject to a regime where males only encountered females for 18 h. Earlier studies showed that flies can respond to artificial selection on the avoidance of an odor previously associated with electric shock (Hewitt et al. 1983) and the extension of the proboscis in response to NaCl preceding the delivery of sugar (Lofdahl et al. 1992). However, another experiment failed to obtain a response to selection for the ability to avoid an odor previously associated with mechanical shock (Kolss and Kawecki 2008). Nonetheless, the general message of those evolutionary experiments is that *Drosophila* has the genetic potential to respond to selection on performance in at least some learning tasks.

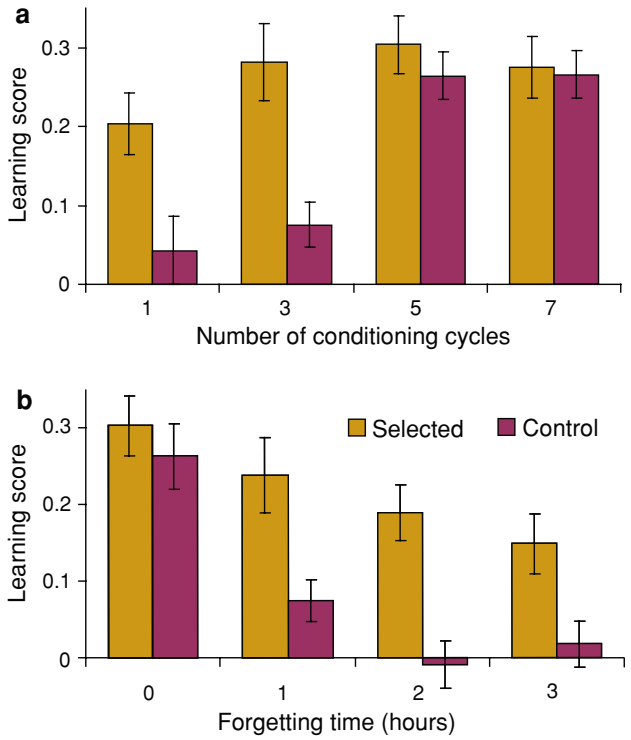

Fig. 3 Experimental evolution of improved learning ability. Learning performances (mean ± SE) of seven populations selected over 40 generations for improved learning ability (*light shading*) and six unselected control populations (*dark shading*). **a** Learning acquisition curve: learning scores as a function of the amount of conditioning (number of conditioning cycles); test immediately following conditioning. **b** Memory decay: learning scores depending on the time between the end of conditioning and the beginning of the test period ("forgetting time"); all flies were subject to five conditioning cycles. Learning was assayed using a modified oviposition learning assay; for details see Mery and Kawecki (2002). Data from Mery and Kawecki (2002)

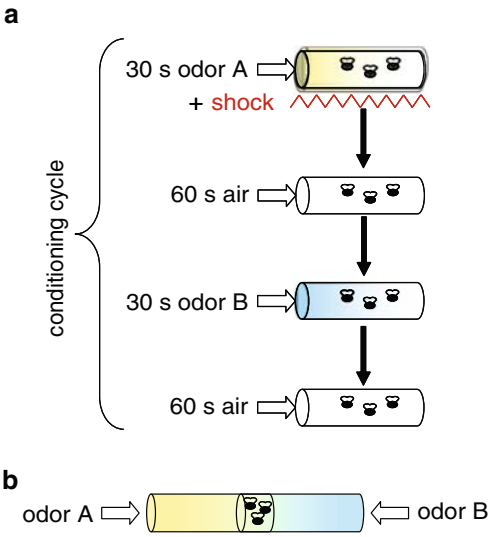

Fig. 4 Schematic representation of the odor–mechanical shock learning assay. **a** Conditioning, **b** test. For details see text

General learning or a specialized task?

Does evolution act on generalized learning processes, or does performance in different types of learning task depend on specialized "cognitive modules" that can evolve more or less independently? This issue is a controversial subject (Healy and Braithwaite 2000; Macphail and Bolhuis 2001), and finding the answer to this question would enhance our understanding of why our species has developed the ability to learn how to ride a bicycle, play bridge, or solve differential equations. These skills could not have directly contributed to the Darwinian fitness of our Pleistocene hunter-gatherer ancestors, so they must be by-products of natural selection acting on some other aspects of learning and intelligence.

Our selected populations were subjected to selection for improved performance in a very specific associative learning task, with orange, pineapple and bitter tastes as stimuli and oviposition substrate choice as the focal behavior. Would their improved learning generalize to other situations, behaviors and stimuli? To address this question, we used another learning assay, in which the flies learn to associate an airborne odor with aversive (unpleasant) mechanical shock (Fig. 4). A group of about 50 flies were placed in a tube with an airflow that could carry odors. During conditioning (Fig. 4a), the flies were first exposed for 30 s to odor A; 4 s after first smelling the odor they were subjected to the first 1 s bout of violent vibrations delivered by a test tube shaker; these bouts of shock were repeated every 5 s while odor A was presented. Thus, odor A signaled imminent danger. Then the shocks ceased and the odor was flushed away by clean air. Subsequently, another odor, B, flowed into the tube for 30 s; this odor was not associated with shock. Another 60 s of clean air completed the conditioning cycle. Such conditioning cycles could be repeated either back-to-back (massed training) or at 15–20 min intervals (massed training). At a desired interval after the end of conditioning, the flies were tested in a T-maze, in which they were given 30 s to choose between the two odors (Fig. 4b). Here, if they have learnt the association between odor A and the shock, they should avoid and preferentially move towards odor B.

The selected populations also performed substantially better in this odor-shock learning assay (Mery et al. 2007). This indicates that the aspects of learning processes that were improved in the course of our evolutionary experiment are not specific to oviposition behavior; nor have the selected flies simply become better about learning about pineapple and orange flavors. Rather, they have become better at associating diverse odors with aversive cues as different as bitter taste and mechanical shock, which rely

on different sensory modalities. Thus, at least in this case, evolution seems to have acted on a relatively general aversive learning ability.

Furthermore, with the odor-shock assay we were able to show that the selected populations showed improvements in long-term memory (Mery et al. 2007). Twenty-four hours after repeated spaced conditioning, the selected flies remembered the association between an odor and the shock better than the controls. Thus, even though in the course of selection it was sufficient to remember an association between fruit flavor and bitter taste for 6 h, the improvement extended to a substantially longer time frame.

Finally, it should be noted that the odor-shock learning assay involves a "classical" or "Pavlovian" conditioning (Rescorla 1988). The flies are exposed to the conditioned stimuli (odors) and the unconditioned stimulus (shock) with no action on their part. This is quite different from the oviposition learning task, where flies have to move towards a fruit odor, land on the substrate and taste it. During such "learning by doing", referred to as "operant" learning (Rescorla 1988), certain behavioral actions are rewarded and become strengthened, while others are punished and therefore become suppressed. In contrast, no behavior is involved in learning acquisition in classical conditioning; i.e., there is no association between a behavior and reward or punishment. It is only during the subsequent test that the learned association between stimuli impinges upon a particular behavior. Classical and operant conditioning are therefore often considered to involve different mechanisms (Rescorla 1988). Our experiment indicates that evolution may act on them together.

Evolutionary costs of learning

The fact that flies can readily evolve improved learning performance in ecologically relevant tasks prompts the question: why have they not used this evolutionary potential for improved learning? One could hypothesize that the benefits of improved learning in fruit flies would not be high enough to compensate for the costs. The ability to learn is a complex adaptation that is likely to be associated with some costs or trade-offs, and so improved learning ability would be favored by natural selection only if the benefits were greater than the costs. Much of the discussion has focused on the costs of acquiring information during learning; i.e., the energy and time spent on the process, and the costs and risks associated with making mistakes (Johnston 1982; Dukas 2004a). However, learning ability may be associated with other costs that are not directly related to the act or learning but rather reflect evolutionary trade-offs between learning ability and other ecologically relevant aspects of the animal's performance. One reason for such trade-offs would be the energetic cost of the central nervous system. Even though the human brain only accounts for about 2% of a human adult's body weight, it consumes about 20% of the total metabolic energy at rest; in infants this share can be as high as 50% (Laughlin 2001). Thus, the brain is an energetically expensive organ, and presumably being able to learn better requires a brain that is larger and more plastic in terms of synaptic connections, and so would presumably require more energy for its development, maintenance and function. However, each individual has only a limited amount of energy and other resources at its disposal, and if more energy needs to be invested in the brain, it must be diverted from other functions such as growth, reproduction, or immune defense. Evolutionary costs of learning could also reflect design trade-offs, independent of energy allocation. For example, it has been speculated that the large size of the human infant brain is a major reason for complications during childbirth, resulting in high mother and infant mortality under preindustrial conditions (Wittman and Wall 2007). It may also have been one reason why humans evolved such that they are born at an earlier developmental stage than other apes.

Evolutionary experiments allow such evolutionary trade-offs associated with learning ability to be addressed directly, by studying evolutionary changes associated with the evolution of improved learning performance. With this aim in mind, we tested whether our fly populations that had evolved improved associative learning performance showed reductions in other fitness-related traits compared to the unselected control populations. Studying such correlated responses to selection is a direct way of addressing evolutionary trade-offs (Roff and Fairbairn 2007). We found no differences between the selected and control populations with respect to egg to adult viability, developmental time, body size, or fecundity at a young age under benign conditions (Burger et al. 2008). However, the "smarter" females showed a faster decline in fecundity with age and lived lives that were 15% shorter than those of the controls (for males the difference was 10%), indicating that they were aging faster (Burger et al. 2008). The trade-off between aging and learning worked both ways: another set of fly populations that experimentally evolved delayed aging were found to learn poorly compared to their corresponding control populations (Burger et al. 2008). Thus, at least some of the relevant loci show antagonistic pleiotropy: alleles that improve learning reduce resistance to the effects of aging and vice versa.

Because in nature flies hardly ever live long enough to show symptoms of aging, the ecological significance of the above trade-off may be marginal. In contrast, another trade-off shown by the selected "smart" flies is likely to be of much greater importance: they suffered from reduced

larval competitive ability. Because the flies from selected and control populations were indistinguishable from each other, it was not possible to study their performance in direct competition against each other—once the flies were mixed it would be impossible to tell who is who. Instead, we studied the competition of flies from each selected and control population against larvae of a strain that carried a *white* mutation, and so were possible to distinguish based on their white eye color. To study their competitive ability, a fixed number of eggs from a given selected or control population were placed in a vial already containing a fixed number of eggs from the white competitor strain and a very limited amount of food. This amount of food was insufficient for all the larvae to complete their development, so that less than half survived to adulthood. The proportion of red-eyed flies among the survivors was used as a measure of the competitive ability of the given selected or control population against the standard white-eyed competitor. Flies from the control populations clearly performed better: they constituted about 80% of the survivors (only 20% were the white-eyed competitors), whereas flies from the selected populations only made up about 55% of the survivors (Mery and Kawecki 2003). One could speculate that this competitive inferiority of the selected populations may be due to a higher inbreeding depression—selection results in a reduced effective population size. Analysis of crosses between replicate selected populations and between replicate control populations excluded this alternative explanation. Rather, the poor competitive performance of the selected populations seems to be due to pleiotropic effects of alleles that were favored by the learning selection regime (Mery and Kawecki 2003).

As for aging, this trade-off between learning ability and larval development under nutritional stress also turned out to be symmetric. In another evolutionary experiment, we bred flies for their ability to develop on food which was very poor. Their adaptation to this nutritional stress involved improved viability and faster development, but, compared to corresponding controls, they showed poorer learning as adults (Kolss and Kawecki 2008).

Thus, the evolutionary experiments with *Drosophila* indicate that evolution of improved learning ability is associated with trade-offs with other ecologically relevant aspects of performance. These trade-offs seem to be symmetric—selection for better learning results in a reduction in larval performance and faster aging, whereas selection for improved larval performance or slower aging results in a reduction in learning ability. These trade-offs also seem to be quite specific—for example, two independent evolutionary experiments indicate that learning ability does not trade-off with resistance to larval parasitoids (Kolss et al. 2006). The next challenge is to gain insights into the mechanisms of those costs.

How learning affects evolution

The ability to learn is a product of evolution acting on genetic variability. However, once learning has evolved in a species, it can affect the relationship between genotype and fitness and so influence how the species evolves in response to natural selection. In particular, thanks to learning, an individual may be able to compensate for inadequacies in its genetically based phenotype with respect to the environment. If so, the ability to learn would reduce the fitness disadvantage of suboptimal genotypes and so reduce the effective strength of natural selection. In such a case, learning would slow down evolutionary change (Johnston 1982; Papaj 1994; Anderson 1995). However, as far back as the end of the nineteenth century, several authors proposed that under some circumstances learning may facilitate evolutionary adaptation to a novel environment (Baldwin 1896; Osborn 1896). First, because of its ability to produce adaptive changes in behavior within a lifetime, learning may allow a population to persist in an environment to which it is initially genetically maladapted, and without learning would go extinct. If the population persists in the new environment, evolution will have time to act on the genetically based behaviors and other traits to bring them closer to the local optimum. Second, under certain circumstances, learning may accelerate evolutionary change. This scenario, known as the Baldwin effect, has been demonstrated in several specific models (Hinton and Nowlan 1987; Fontanari and Meir 1990). Paenke et al. (2007) derived more general conditions for the Baldwin effect: learning will accelerate the response to directional selection if the proportional increase in fitness supplied by learning is greater in individuals that are genetically fitter. In turn, Borenstein et al. (2006) showed theoretically that learning ability may allow a population to cross a "valley" in an adaptive landscape, and so move from one local optimum trait combination to another, potentially resulting in higher fitness.

Despite the long history of this concept and the numerous mathematical models that have focused on it, the Baldwin effect had not been experimentally verified until recently. We took advantage of the learning abilities and suitability of *Drosophila* for experimental evolution to study the effect of learning on the response to directional selection on preference for a new resource (Mery and Kawecki 2004). As in the selection for learning ability, we used oviposition substrate choice as the focal behavior. There were four selection regimes, plus unselected control populations. In the regime "innate orange", the flies in each generation were offered a choice between an orange and a pineapple substrate; the next generation was bred from the eggs laid on the orange substrate. This selection regime thus favored flies that had a stronger genetically based preference for the orange flavor. In the regime "learning orange", the flies

were also selected every generation to oviposit on the orange substrate, but they additionally had an opportunity to learn that orange was preferable. This was done by first offering the flies the orange substrate, together with a pineapple substrate laced with quinine for 3 h. Subsequently, as in the "innate orange" regime, the flies were given uncontaminated orange and pineapple substrates, and eggs laid at this time on orange were used to breed the next generation. The "learning orange" regime was thus identical to the regime described in Fig. 2, except that it was always pineapple that contained quinine in the conditioning period, and only eggs laid on orange in the test period were used to breed the next generation. The proportion of eggs laid by a fly on the orange medium—and thus its contribution to the next generation—reflected an interaction between its innate (genetically based) preference and the influence of its previous experience with quinine-laced (i.e., bitter-tasting) pineapple. The selection regimes "innate pineapple" and "learning pineapple" were mirror images of "innate orange" and "learning orange", respectively: the new generation was always bred from eggs laid on pineapple, and in "learning pineapple" the flies had previous experience with a quinine-laced orange substrate.

If the opportunity to learn slows evolution, the innate preference of flies in the "learning orange" and "learning pineapple" selection regimes should change less during the course of experimental evolution than the preference of flies from the "innate orange" and "innate pineapple" regimes. In contrast, if learning facilitated evolution, the reverse should be the case. Unexpectedly, both outcomes occurred in our experiment, depending on the direction of selection. Of the populations selected to prefer orange, the "innate orange" populations evolved a stronger innate preference for orange compared to the "learning orange" populations (Fig. 5a). Thus, an opportunity to learn slowed down the evolution of genetically based innate preference for the orange flavor. However, for the populations selected to prefer pineapple, "learning pineapple" evolved a stronger innate preference for the pineapple substrate than "innate pineapple" (Fig. 5b), indicating that, for this direction of selection, learning actually facilitated the genetically based response to selection.

These seemingly contradictory results could be explained by considering the effects of learning on the relationship between the genetically based innate preference (the genotypic value as defined in quantitative genetics, Falconer and Mackay 1996) of a given individual and its realized preference quantified as the proportion of eggs laid on the selected substrate (i.e., the phenotype), as illustrated by the following model. Consider an individual facing a choice between two resources, where resource B is of higher quality (Fig. 6); the preference for resource B can be expressed as a number between 0 (complete avoidance of B) and 1 (exclusive use of resource B). In the absence of learning, the realized phenotypic preference corresponds directly to the innate preference (assuming the availability of the resource is not limiting the choice). In this case, a particular difference between individuals in their innate preference (ΔI) maps linearly onto the difference between their realized preferences (Fig. 6). How will learning change the relationship between the innate preference and the realized preference? If the individual already shows a strong innate preference for resource B, there is little scope for learning to increase it further. At the other end of the spectrum, if the individual shows a strong preference for the low-quality resource A, the effect of learning is also likely to be small, for two reasons. First, because the individual prefers resource A to start with, it is not likely that it will sample resource B and thus find out that resource B is actually better. Second, even if it does sample resource B, it may not be easily convinced that B is better than A, because this experience conflicts with its strong innate notion that A should be better. This argument is supported by evidence from phytophagous insects (e.g., Potter and Held 1999), and a similar effect occurs in humans (Ohman and Dimberg 1978). In contrast, an individual with no clear innate preference for one resource over the other will likely sample both equally and will be more amenable to changing its preference as a result of experience. Thus, the effects of learning on the realized resource preference should be greatest for individuals that do not show a strong preference for either resource. Under this scenario, and allowing for a limited amount of learning, the relationship between the innate preference and the realized preference might look like the curve in Fig. 6.

Now consider how learning, in this scenario, affects the difference in realized preference between two individuals whose innate preference values differ by ΔI. If these individuals show moderate innate preferences for resource B, then learning will reduce the difference in realized preference between them ($\Delta L < \Delta I$, Fig. 6a). In contrast, if the individuals initially show preferences for resource A, the one that is initially less biased will change its preference more; i.e., in this case, learning will magnify the effect of the difference in innate preference on the realized preference ($\Delta L > \Delta I$, Fig. 6b). The situation in Fig. 6a may have corresponded to the case in our experiment where orange was the high-quality resource: before the start of the experiment, the mean innate preference for orange was already about 57% (line in Fig. 5a). Thus, learning, which could be used by flies in the "learning orange" regime, would reduce the effect of innate preference on the actual proportion of eggs laid on orange. This would reduce the effective strength of selection on innate preference (note that in our evolutionary experiment the effective contribution to the next generation was proportional to the proportion of eggs laid on the selected resource). In contrast, the initial innate preference

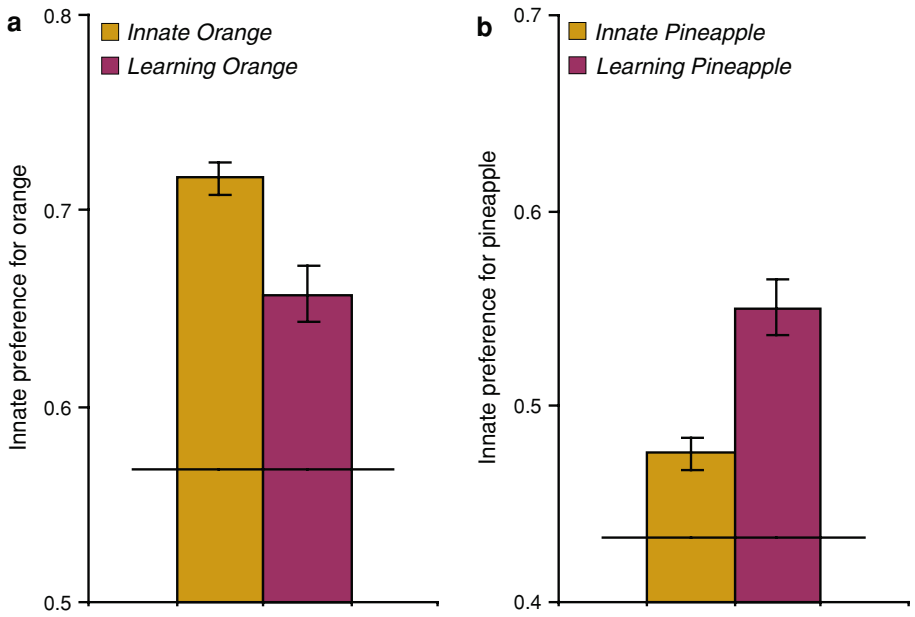

Fig. 5 The effect of learning on experimental evolution or innate resource preference. **a** Populations selected to prefer orange. **b** Populations selected to prefer pineapple. Innate preference scored as the proportion of eggs laid on the focal medium by naïve flies, measured after 23 generations of selection. *Bars* are means ± standard errors based on variation among replicate selection populations (eight per selection regime). The *line* indicates the initial innate preference of the base population (i.e., the baseline). Note that in **a** it is the preference for orange and in **b** the preference for pineapple, so the baseline in **b** equals (1 − baseline) in **a**. For details see the text; data from Mery and Kawecki (2004)

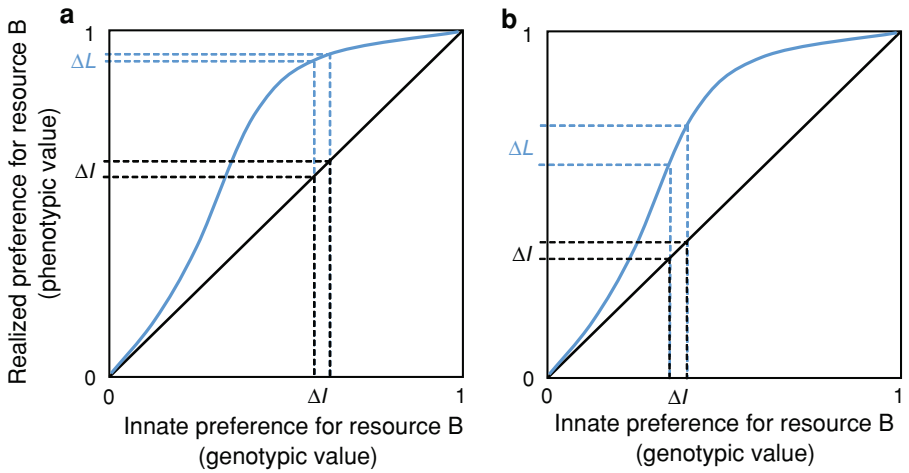

Fig. 6 Graphical model of a hypothetical relationship between the genotypic preference and the realized phenotypic preference. In the absence of learning, the genotypic preference maps linearly onto the realized preference (*diagonal line*). When the animals show some degree of learning, the relationship follows the curve (for justification see the text). Depending on the range of innate preferences, learning may either reduce (**a**) or magnify (**b**) the effect of a small difference in innate preference on the realized preference. Δ*I*: difference in innate preference; Δ*L*: difference in realized preference as modified by learning

for pineapple was only 40%, which would correspond to the situation in Fig. 6b, where learning magnifies the effective selection on the innate preference.

While alternative explanations cannot be excluded (Mery and Kawecki 2004) and this model remains a hypothesis, it illustrates how in principle learning may affect the rate at which a population responds to selection.

Conclusions

The results reviewed above indicate the power of experimental evolution as an approach and *Drosophila* as a model system to address evolutionary questions about learning. Fruit flies are capable of learning in ecologically relevant contexts, such as resource patch choice or mating.

Genetic variation in their populations allows them to evolve, in response to laboratory selection, a substantially improved learning performance within as few as several dozen generations (i.e., 1–2 years). That this potential for improved learning has not been exhausted by evolution in nature can be explained by evolutionary trade-offs for learning, some of which could be identified by studying changes in fitness-related traits correlated with evolution of improved learning. Flies that have recently evolved improved learning performance also offer an opportunity to study the neuronal and genetic bases of those improvements. The fruit fly system also permits experimental testing of hypotheses concerning the interaction between learning and evolutionary change, providing the first direct demonstration of the Baldwin effect.

Even though the brain of *Drosophila* only contains about 10^5 neurons (compared to about 10^{11} in the human brain), and even though its anatomy is very different from that of vertebrate brains, the neuronal mechanisms of learning appear to be highly homologous (Davis 2005). Furthermore, all species are subject to the same forces of evolution. Thus, understanding the evolutionary and molecular aspects of learning in *Drosophila* will give us insights into the processes that have shaped the evolution of learning and intelligence in vertebrates, including us.

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